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ACTIVITIES OF COLONIAL ANIMALS

II. NEUROMUSCULAR MOVEMENTS AND PHOSPHORESCENCE IN RENILLA[1]

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TWELVE TEXT FIGURES AND ONE PLATE (EIGHT FIGURES)

INTRODUCTION

Although Renilla possesses two well-defined colonial movements, both of which may be associated with a certain amount of locomotion, neither of them seems to have excited the attention of investigators to any marked degree. This is probably due to the fact that few workers have had the opportunity of studying living animals. The two movements referred to may be designated as peduncular peristalsis and rachidial peristalsis. These movements, which make up a large part of the general activities of Renilla, have been vaguely noted in various sea-pens by a number of workers (Verrill, '64, p. 13; Musgrave, '09, p. 459), who, however, have not sharply distinguished them. From the accounts given it is clear that rachidial peristalsis in Renilla was seen by Müller ('64, p. 354) and by Eisen ('76, p. 13) and peduncular peristalsis by Wilson ('83, p. 784), who showed the relation of this activity to locomotion especially in young animals. Aside from these few references, however, past publications contain almost no mention of these activities. I shall consider them separately, beginning with peduncular peristalsis.

PEDUNCULAR PERISTALSIS

The extended peduncle in a large individual of Renilla amethystina may measure as much as 7 to 8 cm. in length. In R. reniformis, as Agassiz ('50, p. 208) observed, the peduncle may

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shorten to one-fourth of what was its distended length. If Renillas in a state of contraction are placed in a basin of quiet sea-water, in a short time the peduncles of many of them will show peristaltic waves, which begin not far from the region where the peduncle is attached to the rachis and proceed over the length of the peduncle to its distal end (pl. 1, figs. 1 to 4). These are the waves of peduncular paristalsis (Parker, '19).

Such waves, of which never more than one at a time is seen on the peduncle, pass over that structure with considerable frequency. Thus in a Renilla, that may be taken to represent the normal state, ten waves passed over the peduncle in 360 seconds, hence at the rate of one wave every 36 seconds. The periods occupied by the actual passage of the waves varied from 26 to 28 seconds, and averaged 27.4 seconds; therefore the average resting period for the peduncle as a whole was 8.6 seconds, the difference between 36 and 27.4 seconds. The distance traversed on the peduncle by one of these waves was about 30 mm., and as this distance was covered on the average in 27.4 seconds, it follows that the average rate of progress for the wave over the peduncle was a little less than 1.1 mm. per second. This determination applies to animals in sea-water at a temperature of 23°C. Attempts to ascertain the influence of change of temperature upon this rate were unsuccessful, for colonies of Renilla that were put into sea-water much warmer or much colder than what was normal for them never showed peduncular peristalsis clearly enough to allow of measurement.

Peduncular waves can be seen on excised peduncles, though from the fact that these are not distended with water the waves are less conspicuous than when they are seen in normally attached peduncles. They arise in the severed peduncles at less frequent intervals and with less regularity than in the attached ones. Thus in a severed peduncle they occurred at intervals varying from 110 to 400 seconds instead of every 36 seconds. Because of the collapsed state of such preparations, the moment of their beginning and ending could not be determined with accuracy, hence it is impossible to state their rate under such circumstances. So far as could be judged by the eye, however, the waves traversed

the severed, collapsed peduncles about as fast as they did the distended ones. As a rule, peristalsis is not to be observed on peduncles that have been ligated in a distended condition and then cut from the colony. Apparently this procedure inhibits the movement: In an exceptional case, however, a distended severed peduncle showed peristaltic waves at the rate twelve in 15 minutes or one in 75 seconds, about half as fast as the normal rate, though much more rapid than in the case of severed, collapsed peduncles.

If a contracted Renilla is placed in a shallow aquarium of sea-water that is partly filled with sand, it will usually quickly show peduncular peristalsis and, directing its peduncle downward, it will soon anchor itself in the sand by means of this structure. The peduncular waves running from the attached end to the tip of the peduncle give rise to alternate enlargements and contractions, especially of the distal portion of the peduncle, precisely the kind of movement that is appropriate for burying this structure in the sand It is therefore probable that this form of peristalsis is primarily concerned with the process of sinking the peduncle into the substrate and thereby anchoring the Renilla. It is to be noticed, however, that contracted Renillas as soon as they commence to show peduncular peristalsis not only begin to anchor themselves, but also start to distend. This occurs even when the animal is in a glass basin of sea-water without sand and is thus unable to sink its peduncle. When I first had the opportunity of studying living Renillas, in 1916, I observed the distention of colonies at the same time that peduncular peristalsis was in progress, and as these two processes were invariably associated in the few specimens that I had to work with at that time, I concluded that peduncular peristalsis was an operation by which the colony became filled with water, and not one concerned with anchorage. Since then I have had the opportunity of experimenting on a much larger number of individuals and I have seen specimens of Renilla in which the peduncles have been ligated and cut off fill themselves with sea-water This observation shows that the peduncle is not essential to this operation, as I once believed, and it is my opinion at present that

peduncular peristalsis has to do primarily with sinking the peduncle into the sand and that it is only incidentally concerned with pressure relations in the interior of Renilla whereby distention is accomplished. Individuals that are undergoing inflation very commonly show peduncular peristalsis and inflate more rapidly than those in which the peduncles are quiescent. I, therefore, believe that peduncular peristalsis is an aid in this process, but I am convinced that I was mistaken in my first opinion that this operation is essential to inflation. Inflation apparently depends primarily upon the currents of water generated in the lateral siphonozoöids, currents that, as I have pointed out elsewhere (Parker, '20), are without doubt ciliary in origin.

Peduncular peristalsis is one of the commonest movements in Renilla. If a dozen specimens are made to contract and empty themselves of their contained water and are then placed in a glass vessel of sea-water, within a quarter of an hour half of them perhaps will show peduncular peristalsis. If those showing peristalsis are moved or otherwise disturbed, their activities immediately cease, to begin again only after an interval of quiescence. The operation is, therefore, one freely open to external influences, and yet I have never been able to find any means of exciting it artificially beyond that of causing a colony to discharge its contained water and then allowing it to refill. While this is going on peduncular peristalsis is likely to take place.

Wilson ('83, p. 783) has called attention to the fact that in the young of R. reniformis a peristaltic wave can often be seen passing over the colony from the end at which the rachis is forming to the tip of the peduncle. Each wave results in a forward projection of the peduncle, which thus enables the animal to creep in that direction. The same he says is true of the adults. This statement I can confirm for R. amethystina, for the adults of this species not only anchor and eventually bury themselves in the sand by means of peduncular peristalsis, but they will also slowly plow through the substrate by this means. In the first instance of this kind that I observed the Renilla was in sea-water in a shallow aquarium whose bottom was covered with a few inches of sand. The animal when discovered was

moving very slowly by what was clearly peduncular peristalsis and had left behind it in the sand a trail 6 cm. in length. Subsequently two other instances of a like kind were observed; in one the trail was 21 cm. in the other 24 cm. long. Peduncular peristalsis, therefore, is not only a means of anchoring and even burying the Renilla colony, it is a significant means of locomotion.

RACHIDIAL PERISTALSIS

Rachidial peristalsis differs fundamentally from peduncular peristalsis in the direction its waves take. These begin in the peduncle and spread through the rachis to disappear on the margin of that structure opposite the attachment of the peduncle, a region which, since it corresponds to the apex of the ordinary sea-pen, may be called the apical margin in Renilla (pl. 1, figs. 5 to 8). Thus the direction of rachidial peristalsis is away from the tip of the peduncle, not toward it as in peduncular peristalsis. It is thus easy to distinguish rachidial from peduncular peristalsis, and it is certain that the former was recorded as early as 1864 by Müller in R. Edwardsii and R. reniformis.

Rachidial peristalsis begins in the distal half of the peduncle and spreads over that structure into the rachis, where it appears as a pronounced transverse constriction represented by a right and a left indentation on the corresponding rachidial margins. These indentations proceed slowly around the edges of the rachis till they meet and obliterate each other on its apical margin.

The following records taken from Renillas in sea-water at 23°C. will give a more detailed view of rachidial peristalsis. In one specimen (table 1, A) ten individual waves appeared at intervals varying from 132 seconds to 160 seconds and averaging 146.2 seconds. The period taken by the wave in its passage over the colony varied from 125 seconds to 135 seconds with an average of 130.2 seconds. The resting periods between waves were from 5 to 35 seconds with an average of 16.0 seconds. In a second specimen (table 1, B) the average duration of the wave was 110.5 seconds and of the rest period 21.5 seconds and in a third (table 1, C) 102.5 and 8.5 seconds, respectively. The general averages from these observations show that rachidial waves start about

TABLE 1

Times in seconds in three specimens of Renilla, A, B, and C, for duration of rachidial wave, rest interval, and total interval from the beginning of one wave to the beginning of the next

SPECIMEN	DURATION OF WAVE	REST INTERVAL	TOTAL INTERVAL
A	130	25	155
	125	35	160
	130	10	140
	127	5	132
	130	15	145
	135	15	150
	135	15	150
	135	5	140
	130	15	145
	125	20	145
Averages	130.2	16.0	146.2
B	120	5	125
	120	35	155
	115	10	125
	105	35	140
	105	30	135
	115	10	125
	105	30	135
	105	25	130
	110	15	125
	105	20	125
Averages	110.5	21.5	132.0
C	95	5	100
	90	5	95
	105	5	110
	100	5	105
	105	10	115
	100	20	120
	105	10	115
	110	10	120
	105	10	115
	110	5	115
Averages	102.5	8.5	111.0
General average	114.4	15.3	129.7

once in 130 seconds and pass over the colony in approximately 115 seconds and that the average resting period is about 15 seconds. As may be inferred from what has been stated, never more than one rachidial wave at a time is to be seen on a colony.

In specimen A of those referred to in the preceding paragraph the distance traversed by the waves over the peduncle and rachis measured 148 mm., and as this course was covered on the average in 130.2 seconds, it follows that the rate at which the wave traveled was 1.1 mm. per second. In specimens B and C the respective courses measured 117 and 133 mm., and the rates in these colonies were, therefore, 1.1 mm. per second for B and 1.3 mm. per second for C, or an average of approximately 1.2 mm. per second for all three. This rate is of the same order of magnitude as that already found for peduncular peristalsis, namely, 1.2 mm. per second. The similarity in rate in these two forms of peristalsis indicates that the organization that underlies them must be essentially the same, though reversed so far as polarity is concerned.

The rate of 1.2 mm. per second for rachidial peristalsis was determined in sea-water at 23°C. Efforts were made to ascertain whether this rate was influenced by changes of temperature, but at 15°C., the irregularities in the responses of the colonies were such that measurements were not possible, and at temperatures much above normal no rachidial peristalsis occurred.

The rachidial peristaltic wave ordinarily makes its first appearance in the distal half of the peduncle and spreads thence as a right and a left wave symmetrically over the rachis, at whose apical margin the two waves meet and obliterate each other. If an incision is made on one side of the rachis (fig. 1), the wave passes around this without suffering interruption, even though the cut may reach well toward the center of the colony. Several cuts of this kind may be made in one or both sides of the rachis without interrupting the wave. If a single lateral cut is made from one side of a rachis through its center well toward the other side (fig. 2), the wave that would naturally pass up the incised side is interrupted at the cut, whereas that which traverses the intact side not only reaches the apical margin,

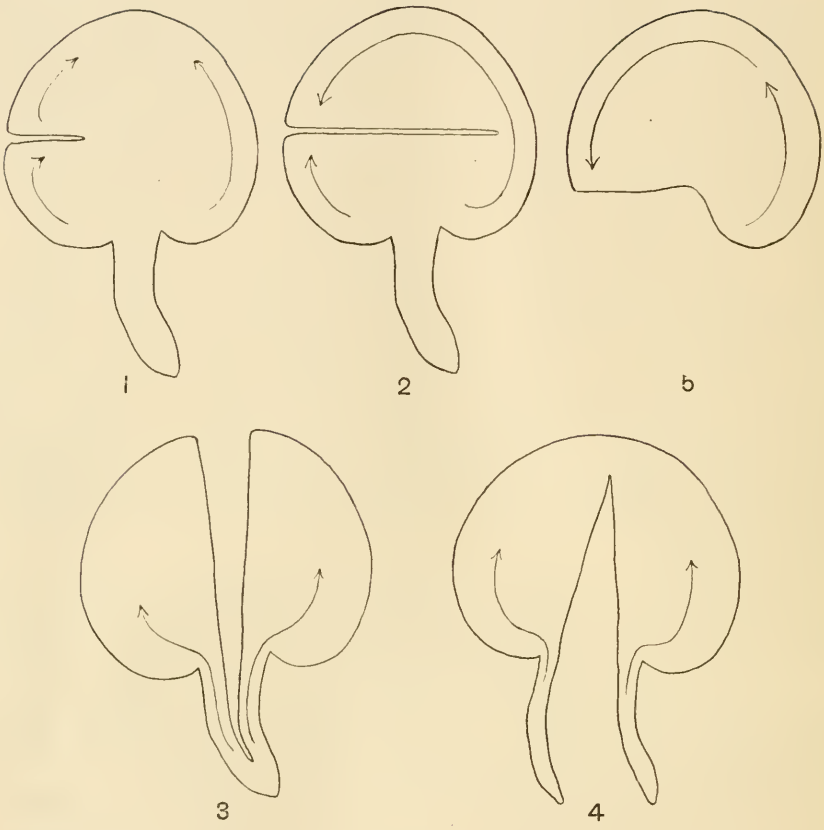

Fig. 1 A Renilla with a shallow unilateral incision in the rachis. The course of the rachidial wave is indicated by arrows.

Fig. 2 A Renilla with a deep unilateral incision in the rachis. The course of the rachidial wave is indicated by arrows.

Fig. 3 A Renilla bisected except for the distal end of the peduncle. The synchronous bilateral, rachidial waves are indicated by arrows.

Fig. 4 A Renilla bisected except for the apical margin. The bilateral rachidial waves, not necessarily synchronous, are indicated by arrows.

Fig. 5 A Renilla rachis devoid of one lobe and the peduncle. The course of the rachidial wave is indicated by arrows.

where it would ordinarily stop, but passes beyond this and down the opposite side to end at the cut. Thus for the latter extent of its course, after it has passed the apical region, it progresses over a part of the rachis in a direction the reverse of that which is normal for this part. If a Renilla is split in its axis from the apical region through its whole extent and the cut is carried well through the length of the peduncle, but not to its distal end (fig. 3), a single wave starts in the peduncle, but is soon represented by a pair of independent but synchronous waves that pass over the two halves of the rachis. If an axial cut is made in the direction severing the two halves of the peduncle completely but leaving the halves of the rachis attached at the apical margin (fig. 4), two entirely independent waves arise, one from each half-peduncle. These waves differ from those in the preceding preparation in that they are not necessarily synchronous. The single peduncular center from which in a normal colony the rachidial wave arises is in this preparation divided into two, and the two half-centers show complete and independent action.

The cutting of incisions not only fails to prevent the formation of a rachidial wave, but considerable parts of a colony may be removed without loss in this repect. Thus, although the rachidial wave ordinarily begins in the peduncle, this whole structure may be ablated without checking the formation of the wave. In a Renilla from which the peduncle has been cut the rachidial wave begins in what was the root of the peduncle and proceeds thence as a pair of waves along either side of the rachis to meet and disappear in a normal way on the apical margin. If instead of cutting off merely the peduncle, the whole center of the rachis is removed, the waves still start synchronously in the adjacent lobes thus produced and progress to the usual termination. If, now, one of the lobes is cut off (fig. 5), the wave as a single wave starts from the remaining lobe and proceeds not only to the apical margin, where it would ordinarily cease, but continues onward around the remainder of the edge of the rachis to the region where the lobe was cut off and ends there. If a preparation is made by cutting off a narrow band around the whole edge of the rachis, this band as well as the remaining central portion will

show rachidial waves. In the band a wave will ordinarily start from each end, the two waves meeting and becoming obliterated near the center, which is really the apical margin. The central portion of a rachis from which the edge has been trimmed will exhibit symmetrical waves like those of a small rachis. If the central part of the rachis is reduced by a delamination of the edge till an area containing only a few zoöids results, this small central area will pulse, though it is almost impossible to distinguish any special direction to its movements. If a preparation is made by cutting off the sides of the rachis and leaving the axis of that part attached to the peduncle, the rachidial wave, when it appears, can be followed from a point close to the distal end of the peduncle over the whole length of that part as well as over

TABLE 2

Intervals in seconds between rachidial waves on the separated right and left halves of a rachis

	NUMBER OF WAVE										AVERAGES
	1	2	3	4	5	6	7	8	9	10	
Right half....	105	115	110	125	120	125	120	115	110	115	115.0
Left half.....	105	125	110	130	115	125	110	115	105	120	116.0

the axis of the rachis to the region of its disappearance on the natural margin.

As might be inferred from the experiments described in the preceding paragraphs, any fair-sized fragment of the rachis of Renilla may exhibit rachidial peristalsis. Thus if a rachis is cut in two lengthwise through its chief axis, the two symmetrical halves will continue to show a rachidial peristalsis in which the waves of the two pieces, notwithstanding their separation, run at very nearly the same rate, as shown in table 2. If the two halves come from a Renilla that is already in rachidial peristalsis and the longitudinal cut is made quickly, the peristalsis is ordinarily not interfered with. After such an operation the two resulting halves not only beat at the same rate, but their waves even keep in phase for a considerable period of time. Of course sooner or later this agreement disappears.

When a Renilla is divided into pieces by cuts transverse to its chief axis, a very different condition from that just described is to be seen. Each piece continues to exhibit contractions, but these contractions have a very different rate in the different regions. Thus in a Renilla cut in two transversely through the center of its rachis the peduncular piece was found to contract on the average once in 115 seconds and the apical piece at the lower rate of once in 205 seconds. The same condition was met with in a Renilla that had been cut into five instead of two transverse pieces (fig. 6). These five pieces may be conveniently designated as the peduncle, the proximal rachis, the middle rachis, the subapical rachis, and the apical rachis, and their several rates of contraction are recorded in table 3.

TABLE 3

Rates in seconds at which one wave follows another in separate transverse pieces of Renilla

PIECES	INTERVALS IN SECONDS BETWEEN WAVES					AVERAGES
Peduncle	125	160	185	170	180	164
Proximal rachis	175	180	190	165	160	174
Middle rachis	205	225	230	200	210	214
Subapical rachis	250	225	230	210	240	231
Apical rachis	280	250	300	260	310	240

As table 3 shows, the peduncular waves have on the average the shortest interval, 164 seconds, and the farther a piece is removed from the peduncle the longer that interval, till the longest one encountered is 240 seconds, in the apical rachis.

It is worthy of note in passing that, excepting the peduncle, the fragments of colonies such as those on which the tests just recorded were made, were easily kept alive in aquaria for fully a week, during which time they continued to exhibit their differences in rate of contraction.

From these and the preceding observations it appears that rachidial peristalsis may take its origin from almost any section of the colony, but that the rates at which the waves emanate become successively lower as one proceeds away from the pedun-

cle and toward the apical margin. In both these respects rachidial peristalsis has a most striking resemblance to the contraction of the vertebrate heart. In this organ, as in Renilla, any part may orignate a contraction, but the rate at which such contraction may arise is different for different parts, being most

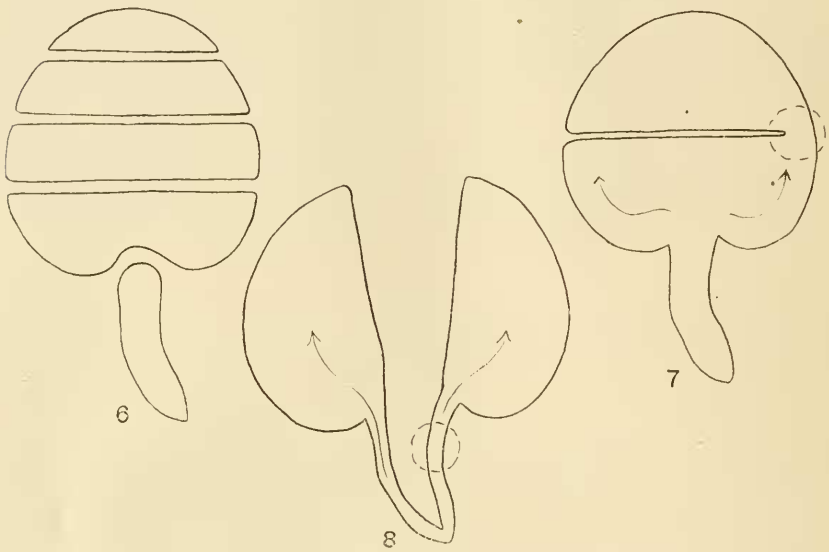

Fig. 6 A Renilla cut into transverse pieces to be tested for the rates at which the rachidial waves originate. The pieces may be designated, beginning at the bottom, as follows: peduncle, proximal rachis, middle rachis, supapical rachis, and apical rachis. (Compare table 3.)

Fig. 7 A deeply incised Renilla in which the connecting bridge of tissue has been treated with magnesium sulphate (dotted circle). The extent of the rachidial waves is indicated by arrows.

Fig. 8 A Renilla bisected except for the distal region of the peduncle. One half-peduncle is treated with magnesium sulphate (dotted circle). The two independent rachidial waves are indicated by arrows.

rapid in the sinus, less so in the auricle, and least so in the ventricle. This has been demonstrated in the vertebrate heart by the same method as that used in Renilla, namely, by cutting the organ into separate pieces and determining the rate of each piece. If, in consequence of its rapidity of action, the sinus of the vertebrate heart may be regarded as the pace-maker for the

whole organ, so the peduncle of Renilla may be looked upon as the pace-maker for the Renilla colony. Thus the peristaltic wave that passes over Renilla has a most striking resemblance to the wave of contraction that sweeps through the cardiac muscle of the vertebrate.

Although the wave of rachidial peristalsis passes from one part to another of the rachis of Renilla so long as there is organic continuity, it can be easily interrupted by anesthesia. If the edge of the rachis of a Renilla on which peristaltic waves are running is covered with crystals of magnesium sulphate, in a short time the waves pass around this region as they do around an incision. If a rachis is cut transversely so that the peduncular portion is connected with the apical portion by only a narrow bridge of tissue over which the peristaltic waves pass and this bridge is then covered with crystals of magnesium sulphate (fig. 7), in a few minutes the waves cease to pass across the bridge. On transferring such a preparation to pure sea-water, the bridge will within half an hour or so again transmit waves. If a Renilla is cut lengthwise on its principal axis so that the halves are connected only by the distal part of the peduncle, the halves, as already stated, will exhibit synchronous waves, which obviously have a common starting-point in the distal portion of the peduncle. If, now, the halves of the split peduncle are spread apart and crystals of magnesium sulphate are applied to one of these arms (fig. 8), the synchronism of the two halves of the rachis soon disappears, showing that one of them, that on the anesthetized arm is no longer under the control of the original peduncular center. On washing off the anesthetic and returning such a preparation to pure sea-water, synchronism in the peristaltic waves begins to reappear in about twenty minutes and is fully reestablished in thirty-five minutes. Magnesium sulphate is an effective temporary means of checking the waves of rachidial peristalsis.

I have been no more successful in exciting artificially rachidial peristalsis than I have been in inducing peduncular peristalsis. If a dozen contracted Renillas are set aside in as many bowls of sea-water and time is given them for partial distention, a number

of them may show rachidial waves and they may then be studied. But aside from this indirect way of inducing the formation of these waves, I know of no special method by which they may be excited. If a Renilla, in which rachidial peristalsis is in progress, is slightly disturbed by being gently handled or even merely jarred, these movements like those of peduncular peristalsis are likely to cease for a time. Thus, although the excitation of rachidial waves was impossible for me to accomplish by external means, their cessation is in this manner easily brought about. The interruption of rachidial peristalsis is almost certain to occur if the stimulus is applied during the brief period that intervenes between waves; it is much less likely to occur if it is applied during the passage of the wave. This suggests another point of similarity between the rachidial wave and a heart beat, for just as the contraction of the cardiac muscle is followed by a refractory period during which the muscle is not open to the reception of a new stimulus, so the passage of a rachidial wave in Renilla prevents the reception of a stimulus which, had it been applied in the period between waves, would undoubtedly have been an effective agent.

Rachidial peristalsis has been referred to by Eisen ('76, p. 13) as a means of locomotion. And it is true that when a Renilla is distended and in sea-water on the surface of the sand, rachidial peristalsis will bring about a movement from place to place. Thus in one example of this kind, a Renilla was observed as a result of ten rachidial waves carried out during twenty-five minutes to have shifted its position 4.2 cm. The movement was of a slow floundering kind and seemed to be the accidental result of the peristalsis rather than a direct and obvious effect of it as implied by Eisen. Although rachidial peristalsis may thus really result in locomotion, I am disinclined to regard it as a real means of locomotion in the same sense that I do peduncular peristalsis.

The real significance of rachidial peristalsis, in my opinion, is not locomotion, but the emergence of the colony from the sand and its distention. After a colony has remained contracted for some time in a sand bank exposed by the falling tide, it is in a condition to reinflate itself on the return of the water. This it

does primarily by the currents of water generated by the lateral siphonozoöids, but the process of distention and the elevation of the colony as a whole is greatly aided by rachidial peristalsis. Thus a contracted Renilla that had more or less buried itself in the sand of the aquarium was seen to begin distending itself by taking in water. In a short time one of its autozoöids had expanded and was projecting through the thin layer of sand that covered the rachis. In half an hour five zoöids had expanded, and in an hour almost all were expanded, whereupon rachidial peristalsis set in and in a short time the whole rachis was full and plump and lifted well above the level of the sand. Thus rachidial peristalsis is apparently a very effective supplement in the process of expansion and may in fact be essential to its completion. At least I have never seen a Renilla reach full and complete distention without exhibiting vigorous rachidial peristalsis toward the close of the operation.

Although neither peduncular nor rachidial peristalsis is essential to inflation, both these processes seem to aid this operation greatly, for in their presence it goes on more rapidly and to greater completion than otherwise. They are both doubtless the means of moving the sea-water contained within the colonial spaces, and thus they may be regarded as important distributors of the fluid supplied by the lateral siphonozoöid. This view of the significance of the peristaltic movements was long ago advocated by Marshall (Musgrave, '09, p. 461).

Peduncular peristalsis takes its origin apparently somewhere in the proximal half of the peduncle. Rachidial peristalsis is initiated in the distal half of that part. Hence the middle of the peduncle is a region that may at one time be occupied by peduncular waves running distally and at another time by rachidial waves running proximally. It is, therefore, not surprising that under normal conditions peduncular and rachidial peristalsis never occur at the same time. In the hundreds of examples of these movements that I have observed in living normal Renillas, I have never seen a single instance in which these two forms of peristalsis occurred on the same individual at once. This relation is a natural one, for, if peduncular peristalsis has to do with

anchoring and burying a colony and rachidial peristalsis with elevating it, it is natural that the two sets of waves should not be running at the same time. In a purely accidental way I discovered a means, however, by which these two operations might be made to occur simultaneously. If a ligature is tied firmly about the peduncle of an inflated Renilla at a position not far from the proximal end of that part and the colony is returned to a basin of sea-water, after an interval of half an hour or more two sets of waves may appear: peduncular waves running over the peduncle distally from the ligature and rachidial waves beginning in the base of the peduncle and passing in the usual direction over the rachis. The simultaneous occurrence of these two sets of waves is due, I believe, to the separation of the colony into two parts by the ligature which is so effective as to bring about a complete physiological dissociation of the regions concerned.

PHOSPHORESCENCE

As early as 1850 Agassiz made the observation that Renilla reniformis "shines at night with a golden green light of a most wonderful softness," a peculiarity which is apparently common to most sea-pens (Mangold, '10–14; Dahlgren, '16). If a fresh specimen of Renilla amethystina that has been exposed to ordinary daylight is carried into a darkroom and stimulated by being prodded gently, no phosphorescence is observable. On trying the same experiment at night, the colony glows with a wonderfully clear blue-green light. During August in La Jolla this phosphorescence made its first appearance about half past eight o'clock in the evening and could be excited any time during the night until toward sunrise.

If during daylight non-phosphorescent colonies are transferred to a dark room and kept there, they begin to show phosphorescence on stimulation in about half an hour and attain what seems to be their maximum capability under these circumstances in from fifty-five to sixty-five minutes. The phosphorescence thus developed seemed never to reach the degree of brightness seen during the night. This is not easy to judge by the eye, but

nevertheless I believe it to be true. It probably rests upon a natural daily rhythm in the animal's metabolism. Phosphorescence induced during the daytime by placing a colony for an hour or so in the dark is completely lost on exposure to daylight for about five minutes. If during the night a colony that shows a naturally acquired bright phosphorescence is illuminated by a strong electric light (40-watt Mazda lamp at 40 cm. distance), the ability to produce light steadily decreases. After five minutes' exposure to light the phosphorescence of the Renilla was obviously fainter than that of another kept in the dark as a check. And after ten minutes' exposure it was very faint in comparison. Continued exposure, however, never totally obliterated the light, showing that either electric light is not so effective in this respect as daylight or that during the night Renilla is more efficient in producing those substances necessary for the production of light than during the daytime. Renilla is then like certain other marine organisms, ctenophores for instance (Peters, '05), which become capable of phosphorescence only in the dark and lose this capacity more or less completely in the light, especially in daylight.

Renilla is phosphorescent only on stimulation. If in the nighttime a spot on the superior surface of the rachis is stimulated mechanically by being prodded or pinched or excited by a faradic current, a series of luminous ripples emanate from it and spread concentrically over the rachis like waves over the smooth surface of a pond into which a pebble has been thrown. If a fine needle point is used as a mechanical stimulus, a single point of light can be excited on the rachis, and this point will glow for some seconds and without becoming a center from which waves emanate, thus showing that in this instance the activity is strictly local. Although the phosphorescence of Renilla can easily be excited by mechanical stimulation, it is noteworthy that the rachidial waves, which were often found running on Renilla in the night and must have produced considerable mechanical disturbance, never excited phosphorescence. If, however, a specimen on which rachidial waves were running was even gently prodded with a rod, waves of phosphorescence would sweep over it uninterruptedly even while the rachidial wave was in progress.

When a glowing rachis is examined under a hand-lens the parts from which the light emanates are seen to be the accumulations of whitish material in which the siphonozoöids are imbedded and which surrounds the bases of the autozoöids. Apparently light emanates from no other source. If the peduncle with the narrow smooth band of tissue leading from this body to the axial siphonozoöid is cut from a Renilla that is capable of phosphorescing, no amount of stimulation either mechanical or electrical will call forth any luminosity in it. No phosphorescence has even been induced on the ventral surface of the rachis. Phosphorescence is quite clearly limited to that part of the dorsal surface of the rachis that is covered by the zoöids, and, as already stated, the particular bodies concerned with luminosity are the small accumulations of light-colored material limited to this region. The observations upon which this statement rests are not as easily and directly made as might be supposed. As the phosphorescence of Renilla is best seen only in complete or almost complete darkness, it is impossible to determine at the time when the light can be seen the exact spot from which it emanates, for the light itself is not strong enough to illuminate the general surface of the rachis. An indirect method of determining the exact parts concerned in light production was therefore resorted to and the various parts of the rachis were tested. For instance, in a dim artificial light, a single autozoöid was cut from a colony and placed upon a glass slide. This was then carried into a dark room, covered with another slide and crushed. Under such circumstances no light was even observed. The same was true of fragments of the purple flesh of the dorsal surface of the rachis. When, however, a group of siphonozoöids with the surrounding light-colored material was crushed, a momentary sparkling could be clearly seen. This was also observed when the light-colored base of an autozoöid was crushed. These two parts were the only parts from which light could be produced in Renilla.

The light material which is thus associated with phosphorescence is seen on close inspection to include two substances: a whitish chalky substance and a light-yellowish crystalline one. Thus in a group of siphonozoöids the central portion is made up

of the whitish chalky material and the peripheral part of the light yellowish substance. These two materials, however, were so intimately associated that it was found impossible either to separate them satisfactorily or to determine by direct inspection which was responsible for the light. In only one region could satisfactory evidence be obtained and that was on the extreme edge of the rachis. Here the two materials form a well-marked double fringe, the outer fringe being composed of the white material and the inner one of the yellowish. This edge, especially when observed from the ventral side of the rachis, shows these two fringes with great clearness, and when phosphorescence occurs, it can be definitely seen that the light is associated with the whitish substance and not with the yellowish one. Hence I conclude that the phosphorescence emanates from the white component of the light-colored masses. The light that this component produces when seen under a hand-lens is indescribably beautiful; it is a combination of intense blue-greens comparable to what one sees in a brightly illuminated opal.

The application of mechanical or electrical stimuli under appropriate conditions to the rachis of Renilla results in what seems to be a series of luminous waves emanating concentrically from the region of stimulation. When one of these wave fronts is closely scrutinized, it is found to be not a continuous line, but a series of luminous points which represent the small masses of white material already alluded to as the source of the light and which for the moment lie in what would be a continuous wave front. Thus the appearance of a wave is due to the momentary glowing of one concentric line of points after another as the impulse that induced the phosphorescence spreads from the center of stimulation outward. This spread of light from the center of stimulation to the rest of the colony in other sea-pens than Renilla was apparently first recorded by delle Chiaje in 1836 (Panceri 71, p. 11).

As with rachidial peristalsis, the waves of luminosity pass around incisions in the rachis, provided these incisions do not completely separate the parts concerned. If the rachis is cut nearly in two transversely, the luminous waves may be started

by mechanical stimulation in either part and will pass thence over the connecting bridge of tissue to the other part. If two symmetrical transverse cuts are made leaving the two parts connected by a narrow axial bridge, the luminous waves will pass from the peduncular to the apical piece or the reverse with perfect freedom. If the region of stimulation is axial in position, the

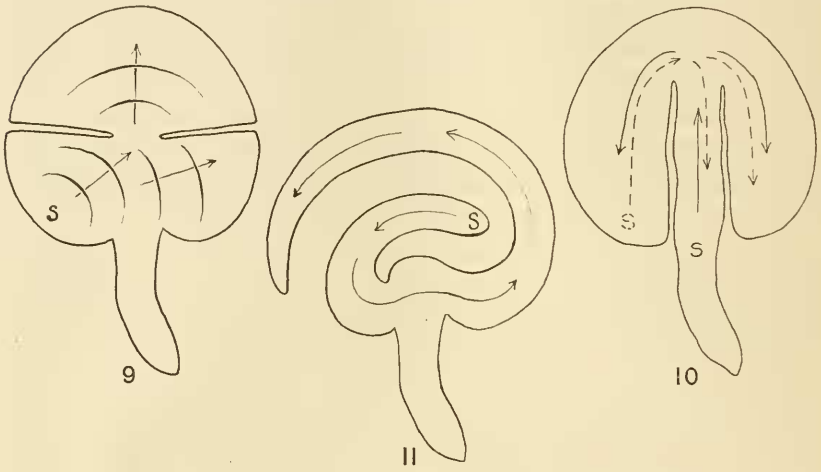

Fig. 9 An almost divided Renilla stimulated at *S* for phosphorescence. The luminous waves in the peduncular portion of the rachis are unsymmetrical; in the apical part, in consequence of the median position of the bridge, they are symmetrical.

Fig. 10 A Renilla partly divided by two longitudinal slits. When the stimulus to phosphorescence is applied in a median position (*S*), the luminous waves have a symmetrical course (solid arrows); when it is applied in a lateral position (dotted *S*), the course is unsymmetrical (dotted arrows).

Fig. 11 A Renilla whose rachis has been cut into a scroll and is somewhat unfolded. A stimulus to phosphorescence applied at *S* is followed by a luminous wave that takes the course of the arrows.

spread of the wave over the stimulated part as well as over the unstimulated one is symmetrical with reference to the axis. If the region of stimulation is lateral to the axis (fig. 9), the spread of the wave is unsymmetrical in the stimulated part, but becomes symmetrical on the unstimulated part in consequence of the symmetrical position of the bridge. If the rachis is cut into three

lobes by incisions that enter it symmetrically from its peduncular margin and it is stimulated at the root of the peduncle (fig. 10), a symmetrical wave of light spreads over the central lobe and into the lateral ones. If a lateral lobe is stimulated, the wave passes to the apical margin and thence onto the other two lobes. If the rachis is cut into a scroll that can be unfolded into an elongated form (fig. 11), stimulation at one end will start a luminous wave that will pass to the other end.

If a colony is split longitudinally through its chief axis and the halves remain attached only through the distal part of the peduncle (as in fig. 3), the stimulation of one half-rachis calls forth a flash of light in that half which, after it has subsided, is followed by another flash in the other half. The second flash follows the first at such an appreciable interval of time that the preparation seems to wink first with one eye and then with the other. In such a test as that just described the interval between flashes is due to the transmission of the wave of excitation through the non-luminous peduncle, for if the peduncle is completely split no such transmission occurs even if the halves of the peduncle are closely applied to each other. This observation shows that the luminous waves are under the control of some form of transmission, non-luminous in character, that spreads in wave-like fashion and for which the phosphorescent waves may be said to be luminous replicas. It also makes clear that the peduncle can transmit the impulses that excite luminosity in the rachis. Not only can the peduncle transmit these impulses, but it can also originate them, for if the distal end of the peduncle of Renilla is pinched, in a moment the attached rachis flashes in waves of phosphorescence. Even when the peduncle is split longitudinally and the cut is carried through much of the rachis toward its apical margin, the stimulation of the distal end of a half-peduncle will call forth in the half rachis of the stimulated side waves of light that pass over quickly onto the half-rachis of the opposite side.

As might be inferred, any portion of the rachis carrying the white material already alluded to can be made on stimulation to glow. Thus right or left halves, apical or peduncular seg-

ments, quadrants, centers, margins, or even minute fragments will on appropriate treatment give out light.

The impulses that induce phosphorescence are profoundly influenced by such anesthetics as magnesium sulphate. If a portion of the rachis of a Renilla is covered with crystals of magnesium sulphate, waves of luminosity can be started in the untreated part and will pass into the treated part for about four or five minutes, after which they will cease on the edge of the treated part, nor will this part give out light even when it is directly stimulated. On washing off such a preparation and putting it in pure sea-water, the power to produce light will return to the treated part in half an hour or so. If a preparation is made by cutting a rachis almost in two by a transverse incision and, after determining that the connective bridge will transmit luminous waves, this bridge is covered with crystals of magnesium sulphate (as in fig. 7), the waves of light will in ten minutes or so be blocked at this point and light will be produced in only that part of the rachis which is directly stimulated. If the edge of a rachis is cut off in the form of a strip 5 to 6 mm. wide and this strip is pinned out in sea-water, waves of phosphorescence can be made to run over it in either direction by appropriate stimulation. If, now, crystals of magnesium sulphate are freely applied to the middle of the strip, the luminosity of the region thus treated begins to decline and, after five minutes, it ceases altogether, though occasional waves that seem to stop on one side of it reappear on the other side. A complete block occurs, however, in from nine to ten minutes and waves of phosphorescence started on one side of the treated area do not reappear on the other. After half an hour in pure sea-water the phosphorescent waves reestablish themselves and pass freely through the region previously anesthetized with magnesium sulphate.

If a V-shaped preparation is made from a Renilla by splitting it through its long axis except at the distal end of the peduncle, it will be found, as already stated, to transmit impulses for light production from one half-rachis to the other through the partly split peduncle. If the unsplit portion of this part is covered with crystals of magnesium sulphate, in five to ten minutes no impulses

to illumination pass through it, for when one half-rachis is excited to glow, the other half-rachis does not follow by producing a flash. Recovery from this condition occurs in such preparations after they have been for half an hour or so in pure sea-water.

The rate at which the luminous waves traverse the rachis of Renilla is a relatively slow one. It, therefore, seemed possible to measure it and attempts were made to carry this out by a photographic method, but the light that emanates from a single phosphorescent wave in Renilla is so faint that the most rapid photographic plates obtainable, even when sensitized for blue-green, were not fogged by it. In this test the plates were exposed to the light without the use of a lens and under water next the source of illumination. Photographic methods were, therefore, abandoned and an attempt was made to determine the rate by the use of a stop-watch and a long strip of phosphorescent tissue. Strips of this kind were cut from the edges of large rachides; they measured 5 to 8 mm. in width and about 10 cm. in length. When first cut they were much contracted, but in an hour or so they relaxed and could be pinned out each in a small wax-bottomed dish of sea-water. After night had come on these strips could be stimulated by touching one end gently with a metal rod, whereupon a single wave of light would start at that end and pass rapidly over the length of the strip to the opposite end. If the stimulus was somewhat irregular, several such waves would pass over the preparation in rapid succession, but with a little attention the application of the rod to the end of the strip could be so regulated that a single wave was invariably called forth. Each wave consisted of a band of light transverse to the long axis of the preparation and with a sharp front edge and a faint rear. The width of the band of light itself in the direction in which it moved was 4 to 6 mm. This band progressed with great regularity from one end of the preparation to the other, and its rate could be taken with fair certainty by a stop-watch. The results of measurements on five such preparations are given in table 4, from which it will be seen that the waves travel on the average 9.24 cm. in 1.25 seconds or 7.39 cm. per second. This rate is close to the determination made on the same phenom-

enon in Pennatula by Panceri ('71), namely, 5 cm. per second, and is approximately sixty to sixty-five times as fast as the rachidial (1.2 mm. per second) and the peduncular rates (1.1 mm. per second). This indicates that the process of transmission that underlies the waves of luminosity is probably entirely different from that which controls peduncular and rachidial peristalsis.

Other evidence that is in favor of the view that these two forms of transmission are essentially distinct is seen in a certain kind of mutual independence that they sometimes show. When

TABLE 4

Times in seconds for the passage of waves of luminosity over strips of Renilla rachis. The stimulus, pressure of a rod, was applied first at the right-hand end of the preparation and then at the left-hand end. Temperature of water 21°C.

SPECIMEN	NUMBERS OF THE TESTS										AVERAGE TIME	LENGTH
	1	2	3	4	5	6	7	8	9	10		
												cm
A	1.0	1.0	1.2	1.4	1.2	1.2	1.2	1.0	1.4	1.0	1.16	9.3
B	1.0	1.4	1.2	1.2	1.2	1.0	1.4	1.2	1.0	1.2	1.18	9.2
C	1.2	1.0	1.4	1.4	1.2	1.2	1.0	1.2	1.4	1.0	1.20	9.3
D	1.0	1.2	1.2	1.0	1.2	1.0	1.2	1.4	1.0	1.2	1.14	9.2
E	1.4	1.2	1.4	1.6	1.4	1.8	1.6	1.4	1.6	1.4	1.58	9.2
General averages											1.25	9.24

a strip of tissue is prepared from the margin of the rachis of Renilla for the measurement of the rate of the phosphorescent waves, it is not uncommon to find that after a time rachidial peristalsis appears on it. When this occurs at night, an interesting comparison between the two sets of waves can be instituted. In one preparation where this occurred, the rate of the rachidial wave was measured and found to be approximately 1 mm. per second. The preparation was then placed in a dim light, and just after a rachidial wave had started from one end that end was stimulated mechanically and a rapid wave of phosphorescence was made to run over the whole strip. On quickly throwing a bright light on the preparation the rachidial

wave that had been observed to start from the given end was now seen to be more than half-way across the strip and progressing uninterruptedly toward the farther end notwithstanding the fact that it had been passed over by a wave of phosphorescence. The passage of these two waves, one rachidial and the other phosphorescent, on the same band of tissue and in a way so that one overtook and outran the other without, however, interfering with it, affords a strong argument in favor of their independence.

The rate at which the wave of luminosity passes over the rachis of Renilla, 7.39 cm. per second, was determined in sea-water at a temperature of 21°C. To ascertain whether this rate is influenced by changes of temperature, two sets of determinations were made, one at 11°, 21°, and 31°C., and another at 15°, 20°, and 25°C. These temperatures were maintained by immersing the strips of rachis pinned out on wax in large vessels of sea-water at the desired temperature. In the initial set the readings were taken first at 21°, then at 11°, next at 31°, and finally as a check at 21° again. In the second set the sequence of temperatures was 15°, 20°, 25°, and 15°C. In both instances the rate characteristic for the first test was recovering after the tissue had been subjected to lower and higher temperatures, showing that these temperatures had not of themselves caused any permanent alteration in the tissues. The results of these two sets of tests are given in tables 5 and 6.

In the first set of determinations (table 5) the average rate per second at 11° was 4 cm.; at 21°, 7.6 cm., and at 31°, 20.7 cm. In the second set (table 6) the average rate per second was at 15°, 6.5 cm.; at 20°, 8.3 cm., and at 25°, 12.2 cm. The relations of these records can best be seen in figure 12, where the two groups are plotted independently. As these plottings show, the two sets of determination lie close together and are reasonably conformable. Their relations are better expressed by slightly curved lines than by straight ones. As is shown in the shorter set, an increase of 10° in temperature is accompanied by an approximate doubling of the rate, 6.5 cm. to 12.2 cm. per second. Judging from the curve itself, the same appears to be true of the longer set except for its upper range. If in this set the rate per

second at 21° is taken to be 7.7 cm., then at 11° half that, or 3.85 cm., should be expected, which is very close to the observed rate of 4.0 cm. per second. On this basis at 31°, a rate of twice 7.7 cm., or 15.4 cm., per second should be looked for, but as a matter of fact the rate at this temperature was found to be 20.7 cm. Aside from this determination, however, all the other rates

TABLE 5

Times in seconds for the passage of waves of luminosity over a strip of Renilla rachis 9.1 cm. long and subjected to the following temperatures: 21°, 11°, 31°, and 21°C. (see figure 12)

TEMPERATURE	NUMBER OF THE TESTS										AVERAGE TIME	RATE PER SECOND
	1	2	3	4	5	6	7	8	9	10		
												cm.
21°	1.2	1.0	1.2	1.2	1.4	1.0	1.2	1.4	1.0	1.2	1.18	7.7
11°	2.0	2.2	2.0	2.4	2.4	2.2	2.4	2.4	2.4	2.4	2.28	4.0
31°	0.4	0.4	0.2	0.4	0.6	0.4	0.6	0.4	0.4	0.6	0.44	20.7
21°	1.0	1.4	1.2	1.4	1.2	1.2	1.0	1.2	1.4	1.0	1.20	7.6

TABLE 6

Times in seconds for the passage of waves of luminosity over a strip of Renilla rachis 9.3 cm. long and subjected to the following temperatures: 15°, 20°, 25°, and 15°C. (see figure 12)

TEMPERATURE	NUMBERS OF THE TESTS										AVERAGE TIME	RATE PER SECOND
	1	2	3	4	5	6	7	8	9	10		
												cm.
15°	1.6	1.4	1.6	1.4	1.2	1.4	1.2	1.6	1.4	1.4	1.42	6.5
20°	1.0	0.8	1.2	1.4	1.0	1.4	1.2	1.4	1.0	0.8	1.12	8.3
25°	0.8	0.6	0.8	0.8	0.8	1.0	0.6	0.8	0.8	0.6	0.76	12.2
15°	1.4	1.2	1.4	1.4	1.6	1.2	1.6	1.4	1.2	1.6	1.40	6.6

are related in the sense that for every interval of 10° the higher rate is approximately twice the lower one. Although the usual interpretation of this condition has been more or less questioned recently, it is generally assumed, in accordance with the Van't Hoff law, that such relations in rates are indicative of chemical rather than of physical processes, an assumption that would aline the kind of transmission that occurs in the wave that con-

trols the phosphorescence of Renilla with the burning of a trail of gunpowder rather than with some form of transmission of a purely physical type.

RESPONSES OF AUTOZOÖIDS

The autozoöids of Renilla are for the most part relatively large polyps scattered to the extent of several hundred over the superior surface of the rachis of the colony. When fully distended they

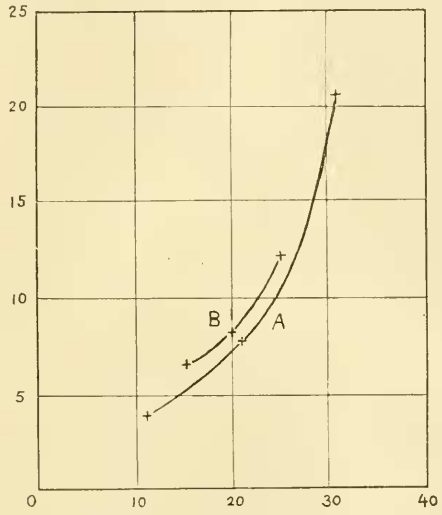

Fig. 12 Plottings of the rates of progression of the luminous waves on marginal bands from the rachis of Renilla as influenced by temperature. Ordinates represent centimeters per second; abscissae centigrade degree of temperature. Plotting A is taken from table 5, plotting B from table 6.

may rise 5 to 6 mm. above the level of the rachis and may have a diameter of as much as $1\frac{1}{2}$ mm. They are delicately transparent and their mesenteries are easily visible through their outer walls. At the distal end each autozoöid has an elongated mouth, the axis of which, as already stated, is related to a structural axis of the colony as a whole. When the zoöid is fully expanded the mouth is seen to be surrounded by white lips from which eight rays pass out corresponding to the mesenteries within and bounding the bases of the eight tentacles. These

tentacles, which are pinnate, are located one at each end of the mouth and three in each of its two sides.

The autozoöids are in some respects remarkably inert. They may be touched, prodded, and even bent from side to side without being brought to contraction; to such treatment they respond like inert elastic bodies filled with fluid under slight pressure. Only after the most vigorous mechanical stimulation can an autozoöid be made to respond by withdrawal.

If they are flooded with weakly acidulated sea-water or with sea-water containing ethyl alcohol, they quickly contract. If they are touched with platinum electrodes, they give no response, but if a faradic current is sent through them, they draw in immediately. They contract on being touched with a naked copper wire, though they do not respond to contact with one that has been dipped in melted paraffin, showing that the reaction to the uncovered wire is probably due to the minute electric currents generated by the unprotected metal (Parker and Van Heusen, '17). To such currents they seem to be especially sensitive.

In withdrawing, the autozoöids sink into pits in the common flesh of the colony. The process of withdrawal ordinarily involves three steps: the folding together of the tentacles, the sidewise bending of the zoöid so that its mouth points usually toward the chief axis of the colony, and the retreat of the zoöid into the zoöid-pit by a process of infolding that begins at the base and eventually involves the whole zoöid. The folding of the tentacles may take place before the bending of the zoöid or the reverse, but in either case these two operations always precede the slipping of the zoöid into its pit. The expansion of the autozoöids is in all essential respects the reverse of their contraction and is brought about apparently by the slight pressure of fluids from within acting on relaxed tissue.

When a single autozoöid is stimulated vigorously by a faradic current, it can be brought to a speedy and full withdrawal, but such stimulus is rarely if ever followed by the contraction of an adjacent zoöid. When such a contraction does occur, it is by no means certain that it is due to the spread of an impulse from the stimulated zoöid, for it happens so rarely that it may be a

spontaneous response of the neighboring zoöid itself and not due to transmission. Even the decapitation of a zoöid with a pair of sharp scissors and the subsequent vigorous contraction of the remaining stump does not seem to affect the neighboring individuals. In a similar manner when one autozoöid or a group of such individuals is fed with minute bits of crab meat or with tow, the zoöids directly concerned open their mouths, but the neighboring ones do not so respond. As a result of many tests of this kind I have come to the conclusion that, though autozoöids are freely open to individual stimulation, they of themselves are not centers from which impulses pass with any degree of freedom to neighboring zoöids or to the colony as a whole.

Although an autozoöid cannot be said to be a center from which impulses pass freely to the rest of the colony, impulses from the general colony reach the autozoöids with great ease. Thus if the distal tip of the peduncle or the dorsal surface of the rachis of an expanded Renilla is touched with a rod, the whole assemblage of autozoöids will quickly withdraw, an operation which is very much less likely to happen when the stimulus is applied to the root of the peduncle or to the ventral surface of the rachis. A faradic current applied to the tip of the peduncle or to the rachis also induces a general withdrawal of autozoöids. These conditions show clearly that stimulation of parts of the colony other than the autozoöids readily excites impulses that reach these polyps, notwithstanding the fact that the converse of this can scarcely be said to be true.

Effective stimuli applied to the tip of the peduncle and to the rachis are not only followed by the withdrawal of the autozoöids, but also commonly call forth more or less general contraction of the whole rachis, a reaction which can likewise be induced by very intense artificial illumination such as that from a powerful arc-light.

This general contraction may result in a discharge through the axial pore of some of the water contained in the colony, but it usually sooner or later passes off and the colony quickly refills itself. The general contraction just described must be due to the activity of the rachidial musculature as a whole, and when

carried to an extreme it temporarily reduces the colony to a mere fraction of its original volume. A stimulus that will bring about a withdrawal of zoöids will not always induce a contraction of the whole colony, so that these two processes must not be regarded as invariably concomitant.

The passage of impulses from any part of the colony into the individual zoöids is not interfered with by making cuts in the colony so long as the resulting pieces still retain organic connections. Incisions may be made to any number or extent and the rachis may be cut into narrow strips or complicated forms, but, so long as organic continuity is retained, impulses will spread from the region of stimulation to the most distant autozoöid and bring about its withdrawal. In short the spread of this form of impulse, so far as experimental pattern is concerned, is exactly like that of the spread of the impulses for phosphorescence. Even in preparations in which the colony is cut almost in two along its chief axis and the halves remain attached only through the distal tip of the peduncle, the stimulation of one half-rachis involves not only the contraction of the autozoöids of that half, but, after a brief interval, the contraction of those of the other half. This reaction suggests that the impulses to zoöid contraction run in waves as do those for phosphorescence, and this is probably true, but the zoöids contract so slowly as compared with the flashing of the phosphorescent points that, under ordinary circumstances, the undulatory nature of the impulse is quite lost sight of.

The impulse to zoöid withdrawal is checked by magnesium sulphate in the same manner as is that for phosphorescence. If a rachis is cut in two except for a small bridge of tissue over which impulses to zoöid contraction can be shown to pass and this bridge is covered with crystals of magnesium suphate, in approximately five minutes the impulses begin to fail to pass and in ten minutes no zoöid contractions occur on one side of the bridge when the other side is stimulated. After about half an hour in pure sea-water, transmission over the bridge of tissue is again resumed. The same kind of temporary block can be established at the unsplit distal end of the peduncle of a partly bisected colony

paralleling in all respects what has been found for the transmission of phosphorescent impulses.

The rate at which the impulse to zoöid contraction traverses the rachis can be measured in much the same way as that for phosphorescent transmisson. When a band of tissue is cut from the edge of a large rachis, pinned out in sea-water, and allowed to remain undisturbed till its zoöids have expanded, a stimulus applied at one end is followed by a wave of contraction that starts among the zoöids at the stimulated end and progresses to those at the opposite end. Although on the uncut rachis

TABLE 7

Times in seconds for the passage of waves of zoöid contraction over strips of Renilla rachis. The stimulus, pressure of a rod, was applied first at the right-hand end of the preparation and then at the left-hand end. The preparations were the same as those used in the determinations given in table 4. Temperature of water, 21°C.

SPECIMEN	NUMBERS OF THE TESTS										AVERAGE TIME	LENGTH
	1	2	3	4	5	6	7	8	9	10		
												cm.
A	1.0	1.0	1.0	1.2	1.0	1.2	1.4	1.0	1.4	1.2	1.14	9.3
B	1.2	1.0	1.2	1.4	1.0	1.2	1.4	1.0	1.2	1.4	1.20	9.2
C	1.0	1.4	1.0	1.2	1.2	1.4	1.0	1.2	1.2	1.0	1.16	9.3
D	1.2	1.2	1.4	1.0	1.2	1.0	1.2	1.4	1.0	1.2	1.18	9.2
E	1.2	1.0	1.2	1.4	1.0	1.2	1.4	1.4	1.4	1.2	1.24	9.2
General averages											1.18	9.24

such waves can scarcely be seen, their presence can be demonstrated beyond a doubt when a long stretch of tissue, such as the band described, is used, and if the interval beween the contraction of the first large zoöid on the stimulated end and that of the last large one on the opposite end is timed, the rate of transmission of the impulse to zoöid contraction can be easily found. The five bands that were used for the determination of the rates of the phosphorescent impulses on the night of August 15th were used again the next morning in daylight for the determination of the rates for zoöid contraction. The results are given in table 7, and it will be seen that the average rate for these five pieces is 9.24 cm. in 1.18 second, or 7.83 cm. per second. This

rate is essentially identical with that obtained from the same bands for the waves of phosphorescence (7.39 cm. per second), and suggests that these two activities, phosphorescence and the withdrawal of autozoöids, are controlled by the same kind of transmission.

Having found that the rate of transmission of the impulse to zoöid withdrawal at a temperature of 21°C. was the same as that for the wave of phosphorescence at the same temperature, an attempt was made to ascertain whether change of temperature influenced the rate of withdrawal as it did that for phosphorescence. But the withdrawal of zoöids is a much less accurately timed operation than the passage of a wave of phosphorescence, and I found it impossible to obtain accurate time readings for withdrawal. At 11°C. the rate at which the withdrawal wave traveled was certainly much slower than at 21°C., but how much slower could not be determined with accuracy In a few instances where the attempted determinations seemed especially clear and decisive the times ranged from 2.6 seconds to 3 seconds for a stretch of 9.24 cm. Assuming the average time to be 2.8 seconds, this yields a rate of 3.3 cm. per second, which is very close to that found for phosphorescent transmission at this temperature, namely, 4 cm. per second. But these determinations were too few in number and too scattering to be relied upon, and the only conclusion that I feel justified in drawing from them is that the rate at 11°C. is slower than at 21°C.

If actual determinations were difficult at 11°C., they were quite impossible at 31°C. At this temperature the wave often seemed much quicker than at 21°C., but its beginning and ending were each so vague and indistinct that it was impossible, even by watching individual terminal zoöids, to obtain any reliable readings. The most that can be said for this aspect of the question is that with increased temperature the wave for withdrawal appears to increase its rate.

When these two forms of transmission, that for phosphorescence and that for zoöid withdrawal, are compared, they are found, as must have been evident from the foregoing account, to be strikingly similar. They both spread through the colony in the

same diffuse way; they are both temporarily interrupted by the action of magnesium sulphate; they have essentially the same rate, and they are both quickened by high temperatures and slowed by low ones. Because of these points of resemblance I believe them to be one and the same thing, a diffuse nervous transmission carried out in all probability by an unpolarized nerve-net. This view is supported by the fact that the rate of this transmission, 7.39 to 7.83 cm. per second, is not far from that for the nerve-net of the sea-anemone Metridium, namely, between 12.1 and 14.6 cm. per second (Parker, '18). In both Metridium and Renilla, however, the rate is relatively low as compared with that found in jelly-fishes, namely, 22.9 cm. per second for Aurelia (Romanes, '78) and 77.5 cm. per second for Cassiopeia (Harvey, '12).

The transmission in Renilla that has just been discussed controls colonial contraction, the general withdrawal of autozoöids, and, at night, phosphorescence. If these three activities depend for excitation upon one nerve-net, it might be supposed that, at least when phosphorescence is possible, all three should invariably occur together and that their independent appearance would be impossible. That they are more or less independent is quite certain. At night a slight stimulus may be followed by a momentary phosphorescence and with no other result. A stronger stimulus involves usually not only phosphorescence, but also the withdrawal of the autozoöids and, if the stimulus is still stronger, general contraction may follow. It, therefore, appears that though these three activities may be controlled by a single nerve-net, they may exhibit a certain amount of independence, for apparently the intensity of the stimulus determines which particular activity or combination of activities may be called forth. Phosphorescence is excited by the slightest provocation; the withdrawal of the zoöids requires a higher degree of activity, and general contraction is produced only by still more vigorous stimulation.

The fact that at night I have never seen general contraction excited without zoöid withdrawal and phosphorescence, and that the stimulus to zoöid contraction is always productive of phos-

phorescence, but not necessarily of general contraction, supports this view. It is, therefore, quite possible that all three activities are controlled by a single nerve-net and yet possess a certain kind of independence, for apparently the strength of the stimulus may determine which particular activity or group of activities may be made to appear.

CONCLUSIONS

The activities of Renilla, as given in this and the preceding paper, show very clearly the main outlines of the organization of this animal. Although its development, as worked out by Wilson('83), gives indisputable evidence of the origin of the colony from a single zoöid and shows that the zoöid is the morphological unit in its composition, its reactions center around the colony as a whole rather than around such units. In this sense the activities of Renilla make plausible the belief of many of the older naturalists that this and other sea-pens are individual animals—a view which from the standpoint of morphology has long since been abandoned.

The Renilla colony fills itself with sea-water through the lateral siphonozoöids and empties itself through the axial siphonozoöid, processes in which the ordinary polyps, the autozoöids, appear to play almost no part. The movement of the water within the colony is chiefly dependent upon the general musculature and particularly upon the two forms of peristalsis shown by this musculature, peduncular and rachidial. As these peristaltic movements, by which the water within the colony is moved, are strictly colonial and as the water enters the colony and emerges from it through particular classes of zoöids, the expansion and contraction of Renilla is a mixed operation, in part zoöidal and in part colonial.

Peduncular peristalsis has for its chief functions the anchoring and burying of the colony and locomotion. These activities are general in character and essentially colonial, not zoöidal. Rachidial peristalsis is the reverse of peduncular peristalsis in that it serves to elevate and expand the colony, but it is like peduncular peristalsis in that it, too, is strictly colonial. In both

forms of peristalsis the waves are so slow, approximately 1.1 to 1.2 mm. per second, that they are much more suggestive of muscular than of nervous activity. And when, as in rachidial peristalsis, the wave movement can be studied in some detail, its diffuse spread, its reversibility, as well as its capacity to originate in any isolated portion of the part concerned, all point to its similarity with the heart-wave in vertebrates. Like this wave, peristalsis in Renilla is probably primarily myogenic, but open to a certain degree of control from a nervous mechanism in which, however, the peristaltic movement does not originate. But whatever may be the details of peduncular and rachidial peristalsis in Renilla, it is perfectly clear that both forms of movement are purely colonial in character and have no direct relation whatever with the zoöids. Hence the expansion and elevation of Renilla and its contraction and withdrawal as well as its locomotion are to be regarded as colonial actions probably of a myogenic origin and surely quite devoid of any zoöidal influence.

If the waves of peduncular and rachidial peristalsis are essentially myogenic, those of phosphorescence have all the appearance of being neurogenic. This is especially striking in their rapidity of transmission, some sixty or sixty-five times that of the peristaltic waves. Apparently they are the product of an unpolarized nerve-net, which serves not only phosphorescence, but also the general contraction of the colony as a whole and the combined withdrawal of the autozoöids. These activities, though they involve the autozoöids, are strictly colonial, for they excite the withdrawal of these zoöids all together and not as individuals and, though they can be readily induced by stimulating almost any part of the surface of the peduncle or the rachis, it is remarkable that they cannot be called forth by stimulating individual autozoöids. Phosphorescence, general contraction, and the withdrawal of the autozoöids, then, are also colonial activities, probably dependent upon a nerve-net and certainly not involving the organization of the zoöid. Such a nervous organization is, as Panceri ('71) long ago stated, social rather than individual.

As all these activities show, the Renilla colony is much more of a unit than it is an aggregate of parts; its morphological constituents, the zoöids, have merged their individuality in that of the colony. Probably this merger is not so profound as it is in the siphonophores, but is it certainly vastly more so than in such a sponge colony as Stylotella, in which the individuals are physiologically quite distinct and apparently only incidentally attached —a state of affairs that is probably reproduced in many of the simple hydrozoan colonies such as Tubularia and the like.

Where colonial organization is highly developed, as in Renilla, many parts of the colony, like the peduncle, the rachis, and the general nerve-net, take on functions that apply strictly to the colony, and in this sense belong to an order superior to that of the colonial unit, the zoöid. These relations are not without a certain morphological interest. The unit of structure in such a colony as Renilla is quite obviously the zoöid. Each zoöid is made up of cells combined into tissues and these into organs. Thus each zoöid exhibits a series of graded relations that are also characteristic of the ordinary metazoan individual. It has long been recognized that most protozoans are unicellular and hence cannot be said in any proper sense to have tissues or organs, for these are always formed by combinations of cells. It is obvious, however, that the single protozoan cell often has special parts that perform particular functions in precisely the same way that the organs of metazoans do. Since these parts cannot be designated as organs, they have been termed organellae. If it is inappropriate to speak of organs in protozoans because this term should be restricted to the multicellular parts of the metazoan individual, it is also inappropriate to use it in reference to a structure in a metazoan colony, even though it may there perform a special function. Thus while it is quite appropriate to designate the tentacle of a zoöid in Renilla as an organ, for it is a multicellular functional unit in a single individual, it is not appropriate to speak of the peduncle of Renilla as an organ, for this is a structure that serves the whole colony of zoöids. Such structures stand above ordinary organs as organs stand above organellae. They might, therefore, be called superorgans. In

Renilla they are represented not only by the peduncle, but by the rachis, the contained nerve-net, and like parts. Such super-organs give a unity to a colony that would be entirely unexpressed in the individuals of which it is composed.

SUMMARY

1. Renilla shows two forms of peristalsis: peduncular, with waves running distally over the peduncle, and rachidial, with waves running in the opposite direction over both peduncle and rachis.

2. In ordinary peduncular peristalsis the waves occurred once every 36 seconds; the time of passage of the waves averaged 27.4 seconds with an average period of rest between waves of 8.6 seconds. The wave progressed over the peduncle at the rate of 1.1 mm. per second.

3. Peduncular waves have been seen on excised peduncles.

4. Peduncular peristalsis is primarily concerned with sinking the peduncle into the sand and thus anchoring the animal. It is also the means of bringing about a complete withdrawal of the animal under the sand and of a certain amount of locomotion. It is secondarily concerned with the distribution of fluid within the animal during distention.

5. In rachidial peristalsis the waves occurred once in about every 130 seconds; the time of passage of the wave averaged about 115 seconds, with an average period of rest between waves of 15 seconds. The waves progressed over the colony at the rate of 1.2 mm. per second.

6. Rachidial waves will pass around any number or variety of incisions in the colony so long as organic continuity is maintained.

7. Separate pieces of Renilla show rachidial waves. When these pieces are from symmetrical regions, they agree in rate; when they are not, the rates are different; the rate is most rapid in the peduncle and least so in that part of the rachis farthest from the peduncle. The peduncle is the pacemaker for the system of rachidial waves.

8. Rachidial waves are temporarily checked by magnesium sulphate.

9. Rachidial peristalsis raises Renilla out of the sand and distributes the fluids contained within its body. It is not concerned with effective locomotion.

10. Renilla is naturally highly phosphorescent at night but not so by day. At night its phosphorescence can be reduced by exposing it to light and by day this can be developed by putting it in the dark.

11. Renilla is excited to phosphoresce only by stimulation, particularly by applying mechanical or electrical stimuli. Concentric waves of phosphorescence emanate from the spot stimulated.

12. Phosphorescence is limited to the upper surface of the rachis of Renilla and is produced by the masses of whitish material that surround the siphonozoöids and the bases of the autozoöids.

13. The waves of phosphorescence pass around any form of incision made on the rachis.

14. The impulses for phosphorescence are transmitted by the non-phosphorescing peduncle as well as by the phosphorescing rachis.

15. The impulses for phosphorescence are temporarily interrupted by magnesium sulphate. At 21°C. they have a rate of about 7.4 cm. per second. Between 10° and 25°C. this rate doubles for each increment of 10°. At 31°C. it is more than double that at 21°C.

16. The autozoöids of Renilla are stimulated with difficulty mechanically, with ease electrically. They are not centers from which impulses pass freely to the rest of the colony, though they are easily entered by impulses from other parts of the colony.

17. Their general withdrawal, due to stimulation of peduncle or rachis, spreads over the colony in a wave which may be temporarily interrupted by magnesium sulphate and which has a rate of 7.8 cm. per second.

18. Peduncular peristalsis and rachidial peristalsis consist of muscular waves whose rhythm is probably myogenic in origin. Phosphorescence, the withdrawal of autozoöids, and general con-

tractions are called forth by impulses, often wave-like in character and probably neurogenic in origin (nerve-net).

19. The activities of Renilla are colonial in scope rather than zoöidal; the zoöid as a unit is dominated by the colony.

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PLATE 1

EXPLANATION OF FIGURES

All figures represent Renilla amethystina Verrill.

1 to 4 Successive phases of the waves of peduncular peristalsis; figure 1, the beginning; figure 2, later stage; figure 3, nearly completed; figure 4, completed.

5 to 8 Successive phases of the wave of rachidial peristalsis.

5 Colony seen from the inferior side with the peduncle elevated and out of focus. The rachidial wave has just started from the peduncle and appears as a pair of indentations on the lobes of the rachis next the peduncle.

6 A later phase of the rachidial wave in which the indentations have reached the midrachis; view of the inferior surface of the colony.

7 Rachidial wave in about the same phase as that seen in figure 6, but viewed from the superior surface.

8 Rachidial wave as a pair of indentations approaching the apical margin, where the indentations will fuse and the wave cease.

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